Morphology and Phyletic Relationship of the Glaucidiaceae

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Glaucidium is different from the Ranunculaceae by (1) pistils grooved along ventral and dorsal sutures and fruits dehiscing along both sutures, (2) thick integuments, the outer one 6 to 13 and the inner one about 5 cell layers thick, (3) staminal traces formed by repeated splitting of receptaclar bundles, (4) centrifugal initiation of stamens, (5) somatic chromosome number being 20, (6) occurrence of coumarin, etc. These and other characteristics are referred to related families. As a result of this, a monotypic new family, Glaucidiaceae, is described, and its phyletic relationship is discussed. The author considers that it is better to include this family in Ord. Hypericales.

Glaucidium, a monotypic genus consisting of *G. palmatum* distributed in Hokkaido, North Honshu and the Japan Sea side of Central Honshu, was described by Siebold and Zuccarini (1845). They classified it in the Ranunculaceae, stating "Die Gattung gehört demzufolge gewiss auch nicht zu den Papaveraceen, sondern reiht sich unter Paeonieen an *Paeonia* selbst an". A. Gray (1859) examined this genus and wrote that "The number of pistils excludes the idea of a relationship with *Podophyllum* and *Diphylleia*, which the foliage suggests. Zuccarini has rightly referred the genus to the Ranunculaceae. It belongs, however, not to the tribe Paeonieae,.... and in my opinion its nearest relative is the Alleghanian genus *Hydrastis*". Since then, it had been generally accepted that *Glaucidium* was closely related to *Hydrastis*.

Prantl (1888) grouped *Glaucidium*, *Hydrastis* and *Paeonia* as a tribe, Paeonieae, which was characterized by an outer integument longer than the inner one, and he expressed his view that "Thatsächlich betrachte ich die Paeonieen als direkte Nachkommen solcher Formen, von denen sowohl die Ranunculaceen als die Berberidaceen ihren Ausgang nahmen". But later, Kumazawa (1938) showed that in *Glaucidium* the outer integument was shorter than the inner one, contrary to the information of Prantl, and the relative length of both integuments does not seem to be so important in the taxonomy of Ranunculaceae. Engler and Gilg (1924) excluded *Glaucidium* and *Hydrastis* from the Paeonieae and created a tribe, Hydrastideae, for them, and Janchen (1949) raised its rank to a subfamily, Hydrastidoideae.

There were several authors who regarded *Glaucidium* and *Hydrastis* as members of the Berberidaceae. Engler (1903), Lotsy (1911), and Langlet (1928) classified both genera in the Podophylloideae of Berberidaceae. Himmelbaur (1913) separated *Glaucidium* and *Hydrastis* from the Podophylloideae and set up a subfamily, Glaucidioideae under the Berberidaceae, and Miyaji (1930) also did so, though he used Hydrastidoideae as the subfamiliar name.

Kumazawa (1930 b, c) considered there was a distinct family, Podophyllaceae, which consisted of 2 subfamilies, i.e., Podophylloideae consisting of *Podophyllum* and *Diphylleia* and Glaucidioideae cosisting of *Glaucidium* and *Hydrastis*. Later (1938 b) he separated Glaucidioideae from the Podophyllaceae and included it again in the Ranunculaceae.

In any case, *Glaucidium* and *Hydrastis* have been considered to be closely related to each other. But the present author (1962 a, 1963) pointed out that *Glaucidium* is not allied with *Hydrastis* and proposed to treat it as a distinct family, Glaucidiaceae. Takhtajan (1966, 1969) accepted the family and put it in the Ord. Ranunculales.

The purpose of the present paper is to describe Glaucidiaceae in detail, to show its particular characteristics, and to discuss its phyletic relationship.

Materials and Methods

The plant materials for this investigation were collected from Minakami, ca. 800 m alt. in Gumma Pref.; Mt. Shirane, ca. 2400 m alt. in Tochigi Pref.; Yunotani, ca. 1200 m alt. in Niigata Pref.; and Mt. Amakazari, ca. 1400 m alt. in Nagano Pref.

Materials for the microscopic observation were fixed in FAA, prepared following the usual paraffine procedure, and stained with hematoxylin or safranin. For the observation of vascular elements, tips of rhizomes were macerated with Schultze's solution.

Observations

The rhizome is well developed, up to 1.5 cm thick, sympodially and rather irregularly elongated, ruggedly branched, more or less crowded, and producing adventitious roots. Sterile and fertile buds conceal a foliar leaf and an aerial stem without radical leaves respectively. The correlation between the position of buds and their fertility is not known. In most cases, vessels in the rhizome have scalariform secondary walls with simple perforations, but sometimes with scalariform, or rarely reticulate perforations (Fig. 1).

The stem is simple, 20 to 40 cm high in flowering stage, 40 to 60 cm high in fruiting stage, being up to 8 mm in diam., solid, usually glabrous, and bearing 3, sometimes 4 cauline leaves at the upper part. Vascular bundles are arranged into 2 rather irregular concentric rings, the smaller ones in an outer ring and the larger ones, descendants of leaf-trace strands, in an inner ring. Xylem is barely concave at the outer edge. Bundle sheaths are arc-shaped on the outside of bundles, but sometimes lignified elements appear also on their opposite sides. At the lower part of the stem, the interfascicular lignified elements appear between the outer vascular bundles. Endodermis is not present.

The leaves are alternate, arranged in 1/2-divergence in appearance. The lower 2 are long petiolate, usually 9-lacunar in nodal type, the upper 1 being sessile, 3–5-lacunar. The petioles are 2 to 15 cm in length in the fruiting stage, bifacial, horseshoe-shaped in cross section, solid, and without any mechanical tissue. The petiolar
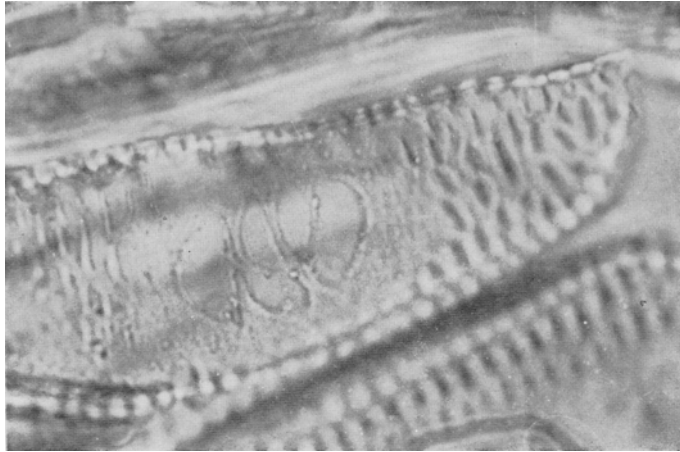
Fig. 1.   Vessel with reticulate perforation. ×1100.

bundles are 8 to 24 in number, arranged radially, and rather irregularly.   Among them, 1 median-dorsal, 2 lateral and 1 ventral bundles are large, and 4 smaller bundles between these.   Besides these bundles, there are 1 to 6 small medullary bundles, whose orientations are irregular (Tamura, 1962 b).   The blades are membranaceous, reniform-rotundate, cordate at the base, and hairy on both sides, especially on the veins.   The hairs are white, being curled on the upper side of the leaves, while more or less spreading on the under side.   Blades of the lower leaves are 7 to 24 cm long, 8 to 27 cm wide, and palmately 7–fid.   Their lobes are acute or acuminate, lobulate and irregularly incised-serrate.   The blades of the upper leaves are 3 to 6.5 cm long, 4 to 8 cm wide, and usually undivided and dentate.

Flower-buds for the coming spring are formed from the beginning to the middle of August.   At first, primordia of perianth-leaves are projected from the flank of the apical dome.   Then stamens are initiated centrifugally, and at last carpels are formed on the raised part of the receptaclar top (Fig. 2).   As soon as the snow melts, the flowering stems elongate and flowering results in May to July.

The flower is solitary.   The pedicels are 0.5 to 3 cm long when in flower, glabrous or sometimes sparcely covered with curled hairs.   The cross section is round in the young stage, but becomes quadrangular later.   The pedicel bundles are roughly arranged into 2 rings.   The inner bundles are larger, 6 to 8, the outer ones smaller, 20 to 30 in number.

The perianth-leaves are 4 in number, broad-ovate or broad-obovate, 3.5 to 5 cm long, 3.5 to 4 cm wide, purple or rarely white, usually 3-lacunar in nodal type, and arranged in decussation.   The outer pair is perpendicular to the distichous rows of cauline leaves. The margins of the paired leaves are barely overlapping with each other in young buds. The stamens are 350 to 500 in number, 4 to 8 mm long, and they initiate and mature centrifugally.   The anthers are elliptic 1.2 to 1.4 mm long, their filaments filiform. The pistils are usually 2, opposite to the outer perianth-leaves, sometimes 1 or 3, con-
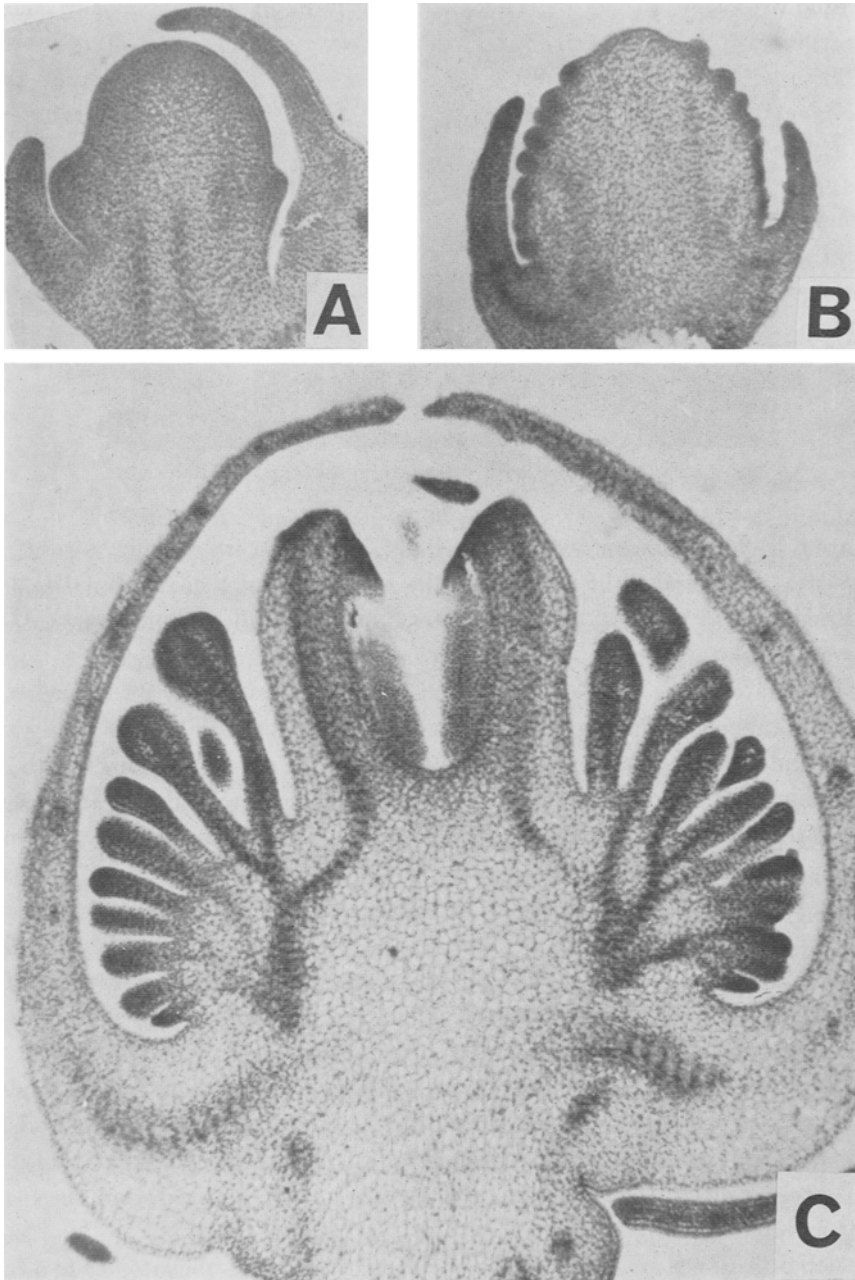
Fig. 2. Development of floral organs. A: initiation of perianth-leaves above 2 developing cauline leaves; B: developing perianth-leaves and centrifugal initiation of stamens. In this stage, initials of carpels do not appear yet; C: further developing flower bud. ×77. A and B collected on Aug. 18, in Minakami, Gumma Pref. and C on Aug. 26, in Yunotani, Niigata Pref.
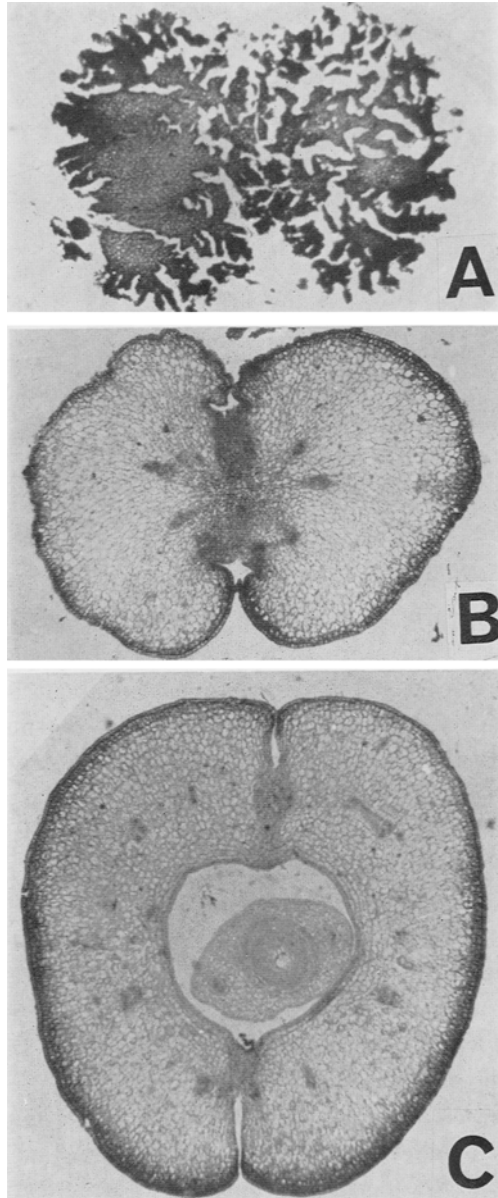
Fig. 3. Cross sections of pistils. A: stigma bipartite; B: style grooved at dorsal (top of figure) and ventral sutures; C: ovary grooved at dorsal (top of figure) and ventral sutures. ×33. A and B in flower, and C after flowering.

nate at the base by the intervention of receptaclar tissue, 6 to 8 mm long including the connate part which is 1 to 1.5 mm long, covered with curled hairs, but becomes glabrate during maturation. There is a distinct furrow along the dorsal suture as well as along the ventral one, where the fruit dehisces. The stigma is bipartite (Fig. 3). The
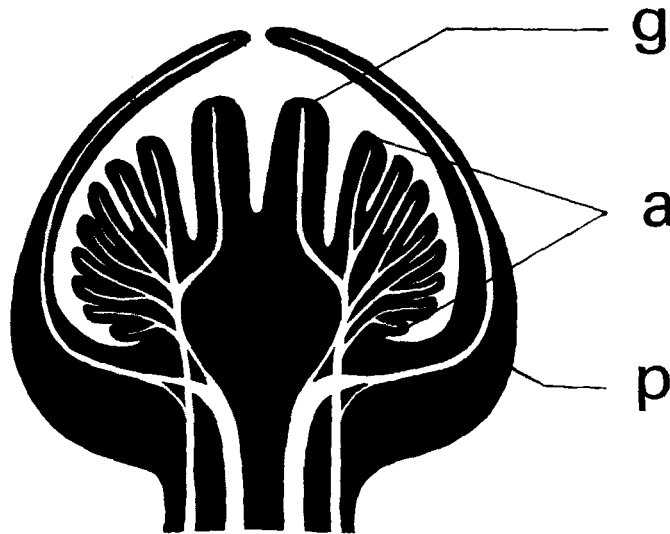
Fig. 4. Diagram showing vascular course in longisection of flower bud. p: perianth leaf; a: stamen; g: pistil.

styles are short. In the early stage of development, before the ovules initiate, the carpels are often bilobed. There are 15 to 20 ovules in one pistil. The integuments are thick, the outer one 6 to 13 cell layers, the inner one about 5 cell layers thick. A distinct bundle runs into the outer integument around the nucellus.

Vasculature in the receptacle is very complicated. A large number of bundles of the inner ring and some of the outer one in the pedicel enter the perianth-leaves. After their departure, 16 to 24 bundles remain in the receptacle and arrange in a circle. These are derived mainly from the outer bundle ring and partly from the inner one of the pedicel. They are extended or divided into 2 or 3 strands in the radial direction. As they pass to the periphery, they are further divided or branched radially or lateral-ly, sometimes anastomosing, and then become the staminal traces. The remaining bundles often fuse to their neighbouring ones, and divide laterally, and further split as to form the staminal traces. A regular network of vascular bundles is not observed in the receptacle. After departure of the staminal traces, the 10 to 12 remaining bundles become arranged as an aggregate in the shape of an ellipse near the center of the receptacle, leaving 2 bundles on opposite ends of the long axis of the ellipse. Each of these 2 bundles become the dorsal bundle of the corresponding pistil. The mass of bundles aggregated in the center divide into 2 parts, each of which enters into the corresponding pistil. These divide again, forming the 2 ventral bundles of the pistil. In an early stage of bud development, only the dorsal bundle is differentiated. In a longisection of the flower bud, the outer bundles of the pedicel run straight up into the receptacle and enter the stamens situated at the uppermost part of the receptacle. Their branches bent outward enter the stamens situated at the lower part of the recep-tacle, and those bent inward enter the two pistils (Fig. 4).

After flowering, as the connate parts of both pistils develop, the receptaclar tissue
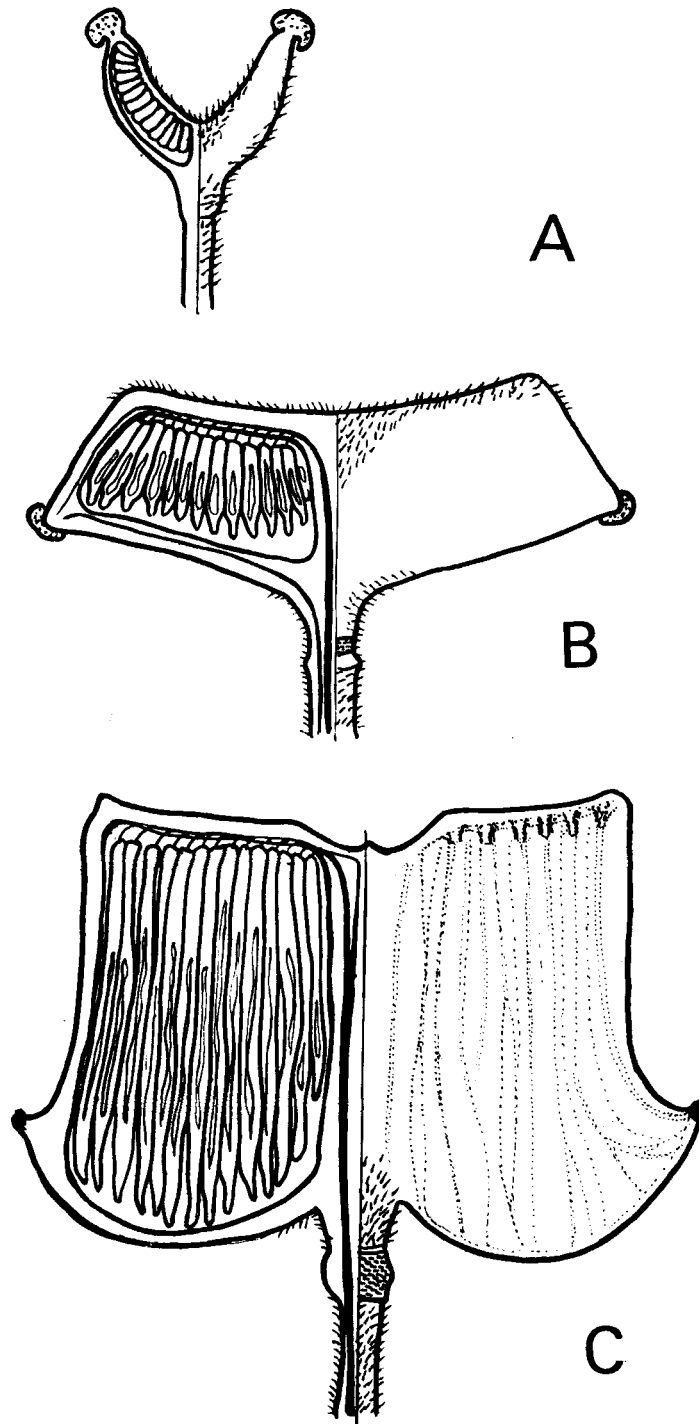
Fig. 5. Development of pistils. A: in flower; B: after flowering; C: in mature condition. Section of pistil (left side) showing development of ovules. ×3.
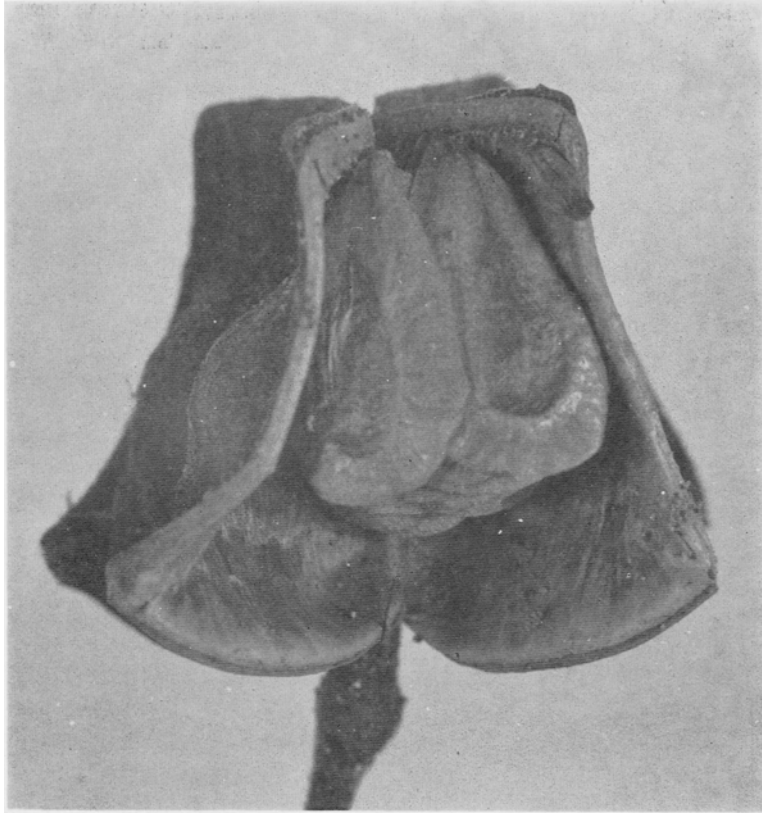
Fig. 6.   Fruit showing dehiscence along dorsal and ventral sutures. ×3.5.

supplied with bundles continues to grow.   At this stage the bundles become 12 to 16 in number, 4 of which are large.   These bundles run up through inserted tissue to the top of the connate part, and then diverge to enter the fruits as a pair of ventral bundles from which seminar traces depart.   At the part where the uppermost ovule is attached, the ventral side of the pistil projects, its development occurring simultaneously with that of the seeds.   Accordingly, pistils become divaricate and long quadriform in side view (Fig. 5).   The outer integument develops into a wing, and the nucellus and inner integument almost degenerate.

The follicles dehisce along both the ventral and dorsal sutures, and are quadriform, connate along the inside of both, being about 16 mm in length.   The dorsal suture turns down more or less convex about 17 mm long.   The lower part of ventral suture where seeds are attached turns upside about 13 mm long, while the upper part where no seeds are attached turns abruptly outward about 13 mm long (Fig. 6).   Veins of the pericarp run parallel between the lower and upper margins, though they often branch and anastomose.

The seeds in any one fruit are 18 to 20 in number, obovate, broadly winged, 12 to 14 mm long, 9 to 10 mm wide including the wing which is 2 to 3.5 mm wide.   There is

Fig. 7. Seed. Seed coat and endosperm partly removed to show embryo. ×4.

a distinct bundle in the wing. The endosperm is about 5.5 to 6 mm long, 3.5 mm wide and 1.5 mm thick. The embryo is 4.5 to 5 mm long, and completely mature, at least morphologically, when the seeds detach (Fig. 7). The hypocotyl and radicle are about 0.6 mm long and thick. The petioles of the 2 cotyledons are united together, and are about 1.5 mm long, 0.6 mm thick, with laminae about 2.7 mm long and 2.3 mm wide. The vascular system in the hypocotyl is divided into 4 strands at the region near the cotyledonary node. Two of these enter the cotyledons as their corresponding middle bundle, while the other 2 divide into 2 and serve as their lateral bundles. Cells of the central part of fused petioles are small in diameter and more or less elongated longitudinally.

Discussion

Many features of *Glaucidium* as described above are improper for those of the Ranunculaceae. Among them, the followings are especially important phylogenetically. (1) The pistils and fruits are grooved along both ventral and dorsal sutures and dehisce along these grooves. The follicles of the Ranunculaceae dehisce along the ventral suture only. (2) The integuments are thick, the outer one 6 to 13 cell layers and the inner one about 5 cell layers thick. In the Ranunculaceae, the integuments are about 8 cell layers thick at the most whether they are double or single (Kumazawa, 1938 a). (3) The staminal traces are formed by repeated splitting of the receptaclar bundles. In the receptacle of the Ranunculaceae, a regular network of bundles is formed (Smith, 1926, 1928). (4) The stamens initiate and mature centrifugally, contrary to their centripetalous initiation and maturation in the Ranunculaceae. (5) The chromosomes are small and 20 in somatic number (Miyaji, 1927; Kurita, 1957). Such number, as well as 5 in basic number, is not found in the Ranunculaceae. (6) A large amount of

glaupalol, a substance with a coumarin skeleton, is present (Irie *et al.*, 1967; Murakami *et al.*, 1967). No alkaloid is detected. Coumarin is not found in the Ranunculaceae. These differences clearly suggest that it is unreasonable to include *Glaucidium* in the Ranunculaceae.

Besides the above mentioned differences, the following features are also significant in distinguishing *Glaucidium* from the ranunculaceous genera. (1) The bud scales, usually 4 in number, and cauline leaves are arranged distichously in appearance and the perianth-leaves are decussate. (2) When sprouting, the leaves are wrinkled and the margins of the folded lateral lobes are piled alternately and more or less irregularly (Kumazawa, 1937 b). (3) Two pistils occur, which are connate at the base by insertion of the receptaclar tissue, and the connate part elongates after flowering. (4) The seeds are large with a wide wing. (5) The pedicels have medullary bundles derived from perianth-leaf traces. (6) The stamens are enormous in number. This may be related with the branching of the receptaclar bundles which produce the staminal traces. (7) The vessels sometime have scalariform or reticulate perforations. (8) A distinct intraseminar bundle is present. (9) The embryos are completely mature, at least in size and shape, when the seeds become detached. In geophilous perennials of the Ranunculaceae, embryos are usually immature at this stage. (10) The xylem in the cauline and petiolar bundles is not as distinctly V-shaped as it is in the Ranunculaceae. (11) In the petioles, there are several small medullary bundles and no mechanical tissues. These above differences of features are ones of quantity, or else they occur rarely in the Ranunculaceae. It may happen that two or three of them occur in a species of the Ranunculaceae. However, it is quite difficult to imagine that so many unusual features could occur together in a single species. This conclusion supports the view that *Glaucidium* must be excluded from the Ranunculaceae.

Glaucidium, Hydrastis, Podophyllum and *Diphylleia* have many common characters as follows: (1) a well-developed creeping rhizome, (2) a single radical leaf on the end of the rhizome, (3) flowering stems having no radical leaves but scales at the base, (4) foliar cauline leaves few in number and arranged in 1/2-divergence in appearance, (5) medullary bundles in the stem and petioles, (6) bundle sheaths of the Anemone-type (Kumazawa, 1930 a) and almost absence of secondary xylem in the stem, (7) a tendency for cotyledonary fusion, (8) the aerial organs produced in the first year of germination are restricted to cotyledons, and the first leaf is scaly (Kumazawa, 1930 a, b). Pollens of *Glaucidium, Hydrastis* and *Podophyllum* are ellipsoidal with 3 furrows parallel to the long axis, while those of *Diphylleia* have many germinating pores (Kumazawa, 1937 a). In contrast, *Podophyllum* and *Diphylleia* differ from *Glaucidium* in the following points. In the former, (1) regular sympodial rhizomes are formed as the result of the elongation of the axillary bud at a definite node, (2) scales of the winter bud are arranged in nearly 2/5-divergence, (3) leaves are peltate, (4) latent axillary buds concealed in the fertile winter bud become aerial after 2 winters, (5) bundles are scattered in the stem, (6) in rhizomes, the interfascicular cambium is not formed and secondary tissues are poorly produced; on the other hand, in the rhizomes of

Glaucidium, secondary tissues are richly produced by the interfascicular cambium. As a result the epidermis and the outer part of the cortex peel off and the outermost layer of the adult rhizome is a pseudodermis formed successively (Kumazawa, 1930 b, c), (7) perianth-leaves and stamens are trimerous, (8) pistils are single, (9) fruits are berries, (10) seeds are not winged, (11) the outer integument is made up of about 5 cell layers and the inner one of 2 cell layers in thickness (Kumazawa, 1938 a), (12) coumarin is not reported, (13) *Diphylleia* contains a substance showing an antimitotic effect similar to that of podophyllin contained in *Podophyllum*, but *Glaucidium* does not contain such substances (Toyokuni and Toyokuni, 1964), and (14) chromosomes are large, 12 or 16 in somatic number (Langlet, 1928). Accordingly, it does not seem that *Glaucidium* is phyletically related to *Podophyllum* and *Diphylleia*, much less to other herbaceous berberidaceous genera. The resembrances in general habits and vegetative morphology may be caused by the fact that these plants grow under similar environmental conditions.

Hydrastis has commonly been treated together with *Glaucidium*, and both genera have been classified as members of the same group. But, such treatment appears to be incorrect. In *Hydrastis*, in contrast to *Glaucidium*, (1) pistils are numerous, free, with 2 ovules, which become 1-seeded berries, (2) perianth-leaves are 3 and caducous, (3) pedicels have no medullary bundles, (4) vasculature in the receptacle is rather simple and regular as in the members of the Ranunculaceae, (5) stamens may be initiated centripetally, (6) integuments consist of about 8 cell layers in total as in usual ranunculaceous genera (Kumazawa, 1938 a), (7) seeds are globose, not winged, (8) young sprouting leaves are not wrinkled, and their lobes are folded inward independently and arranged palmately (Kumazawa, 1937 b), (9) chromosomes, though small, are 26 in somatic number (Langlet, 1928), and (10) coumarin is not reported. These characteristics are common to or at least not conflicting with those of the Ranunculaceae, an exception being the chromosome number. In *Hydrastis*, the outer integument is longer than the inner one as in the Berberidaceae, while in the Ranunculaceae, the outer integument is usually shorter than or, at the most, as long as the inner one. Eames (1961) pointed out that the vessels of *Hydrastis* have scalariform perforations and scalariform pits on their lateral walls in contrast to the simple perforations and rounded pits in the case of Ranunculaceae. He tended to separate *Hydrastis* from Ranunculaceae and to give it a family rank as Hydrastidaceae. Takhtajan (1969) accepted this treatment. Even if the Hydrastidaceae is accepted as a distinct family, it is very close to the Ranunculaceae and lies somewhere between the Ranunculaceae and the Podophyllaceae.

There seems to be no room for doubt that it is unreasonable to retain *Glaucidium* in the Ranunculaceae, and a monotypic family, Glaucidiaceae should be accepted. Accepting this, there remains the problem of the systematic position of the Glaucidiaceae. As mentioned above, the differences between the Glaucidiaceae and the Ranunculaceae or other related families such as Hydrastidaceae, Podophyllaceae, etc. are so remarkable that it is difficult to assume a close relationship between the

Glaucidiaceae and any of these ranalian families. The phyletic relationships of the Glaucidiaceae still remain in question, but numerous stamens initiated centrifugally, staminal traces formed by splitting of the receptaclar bundles, thick integuments, occurrence of 3 pistils, vessels with scalariform or reticulate perforations, etc. seem to suggest an affinity of the Glaucidiaceae to the Paeoniaceae. It seems that the centrifugal initiation of stamens is not so important phyletically as considered before, because such a mode of stamen initiation is found in many families belonging to different orders. It is not clear whether particular phenomenon known to occur in the embryogenesis of *Paeonia* (Yokovlev and Yoffe, 1957; Cave *et al.*, 1961) is found in *Glaucidium* or not. Further more, both genera are different from each other in the vasculature of their receptacles. That is, in *Paeonia*, a large part of the pedicel bundles of the inner ring enters pistils (Sawada, 1971), while in *Glaucidium* they enter perianth-leaves. In the present treatment, the author considers that it is better to put the Glaucidiaceae in the Ord. Hypericales, whether the Paeoniaceae are included in the order or not, than in the Ord. Ranunculales.

   Glaucidiaceae, fam. nov. (Ord. Hypericales)

   Perennis, rhizomate bene crescente. Caulis uniflorus, 3~4–foliatus. Folia inferiora palmatifida grosse serrata. Tepala 4. Stamina numerosa initiant centri-fugaliter. Fasciculi staminum formantur saepius ramificatis fasciculis receptaculorum. Pistilla 2, interdum 1 vel 3, base connate; matura quadriformia, dihiscentia ad suturas ventralis dorsalisque. Integumenta crassa. Semina late alate albuminosa. Chromo-soma 20 in numero somatico. Coumalina abundanter continetur.

   Familia monotypica. Typus: *Glaucidium*.

References

CAVE, M.S., H.J. ARNOTT AND S.A. COOK. 1961. Embryogeny in the California peonies with reference to their taxonomic position. Amer. J. Bot. **48**: 397–404.

EAMES, A. 1961. Morphology of the Angiosperms. McGraw-Hill, New York.

ENGLER, A. 1903. Syllabus der Pflanzenfamilien, 3. Aufl. Gebrüder Borntraeger, Berlin.

———— AND E. GILG. 1924. Syllabus der Pflanzenfamilien, 9. Aufl. Gebrüder Borntraeger, Berlin.

GRAY, A. 1859. Diagnostic characters of new species of phanerogamous plants, collected in Japan by Charles Wright. Mem. Amer. Acad. Arts and Sci. **6**: 379.

HIMMELBAUR, W. 1913. Die Berberidaceen und ihre Stellung im System. Denkschr. Akad. d. Wiss. Wien, Math.-naturw. Kl. **89**: 733–796.

IRIE, H., S. UYEO, K. YAMAMOTO AND K. KINOSHITA. 1967. The structure of glaupalol, a novel furanocoumarin from *Glaucidium palmatum* Sieb. et Zucc. Chem. Commun. 1967: 547–548.

JANCHEN, B. 1949. Die Systematische Gliederung der Ranunculaceen und Berberidaceen. Denkschr. Akad. d. Wiss. Wien, Math.-naturw. Kl. **108**: 1–82.

KUMAZAWA, M. 1930 a. Studies on the structure of Japanese species of *Ranunculus*. J. Fac. Sci. Tokyo Univ. Sect. 3, **2**: 297–343.

————. 1930 b. Morphology and biology of *Glaucidium palmatum* Sieb. et Zucc. with notes of affinities to the allied genera *Hydrastis*, *Podophyllum* and *Diphylleia*. J. Fac. Sci. Tokyo Univ. Sect. 3, **2**: 345–380.

————. 1930 c. Structure and affinities of *Glaucidium* and its allied genera. Bot. Mag. Tokyo **44**: 479–490.

————. 1937 a. Pollen grain morphology in Ranunculaceae, Lardizabalaceae and Berberidaceae. Jap. J. Bot. **8**: 19–46.

————. 1937 b. Comparative studies on the vernation in the Ranunculaceae and Berberidaceae. J. Jap. Bot. **13**: 573–586, 659–669, 713–726.

————. 1938 a. On the ovular structure in the Ranunculaceae and Berberidaceae. J. Jap. Bot. **14**: 10–25.

————. 1938 b. Systematic and phylogenetic consideration of the Ranunculaceae and Berberidaceae. Bot. Mag. Tokyo **52**: 9–15.

KURITA, M. 1957. Chromosome studies in Ranunculaceae xxv. Mem. Ehime Univ. Sect. II, Ser. B, **5**: 165–169.

LANGLET, O. 1928. Einige Beobachtungen über die Zytologie der Berberidazeen. Svensk Bot. Tidsk. **22**: 169–184.

LOTSY, J.P. 1911. Vorträge über botanisches Stammengeschichte **3**: 578–594. Gustav Fischer, Jena.

MIYAJI, Y. 1927. Über die somatischen Chromosomen einiger Ranunculaceen. Bot. Mag. Tokyo **41**: 568–569.

————. 1930. Beiträge zur Chromosomenphylogenie der Berberidaceen. Planta **11**: 650–659.

MURAKAMI, T., Y. MIKAMI AND H. ITOKAWA. 1967. Die Struktur des neu isolierten Glykosids aus den Rhizomen von *Glaucidium palmatum*. Chem. Pharm. Bull. **15**: 1817–1818.

PRANTL, K. 1888. Beiträge zur Morphologie und Systematik der Ranunculaceen. Bot. Jahrb. **9**: 225–273.

SAWADA, M. 1971. Floral vascularization of *Paeonia japonica* with some consideration on systematic position of Paeoniaceae. Bot. Mag. Tokyo **84**: 51–60.

SIEBOLD, P.F.V. AND J.G. ZUCCARINI. 1845. Florae Japonicae familiae naturales. Abh. Akad. Muench. **4–2**: 184.

SMITH, G.H. 1926. Vascular anatomy of Ranalian flowers I. Ranunculaceae. Bot. Gaz. **82**: 1–29.

————. 1928. Vascular anatomy of Ranalian flowers II. Ranunculaceae (Continued), Menispermaceae, Calycanthaceae, Annonaceae. Bot. Gaz. **85**: 152–177.

TAKHTAJAN, A. 1966. Systema et phylogenia Magnoliophytorum. 100. Soviet Publishing Institution, Nauka, Moscow.

————. 1969. Flowering plants, origin and dispersal. 205–239. Translated by Jeffrey, C., Oliver and Boyd, Edinburgh.

TAMURA, M. 1962 a. Taxonomical and phylogenetical consideration of the Ranunculaceae. Acta Phytotax. Geobot. **20**: 71–81.

————. 1962 b. Petiolar anatomy in the Ranunculaceae I. Sci. Rep. Osaka Univ. **11**: 19–47.

————. 1963. Morphology, ecology and phylogeny of the Ranunculaceae I. Sci. Rep. Osaka Univ. **11**: 115–126.

TOYOKUNI, H. AND Y. TOYOKUNI. 1964. Ein neuer Anhalt für die Teilung der Podophyllaceen in zwei Unterfamilien. Bot. Mag. Tokyo **77**: 197–198.

YAKOVLEV, M.S. AND M.D. YOFFE. 1957. On some peculiar features in the embryology of *Paeonia* L. Phytomorphol. **7**: 74–82.